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The effects of experimental bait collection and trampling on a *Mytilus californianus* mussel bed in southern California

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Abstract Rocky shores in southern California are heavily visited by humans. At sites used by recreational fishers, the effects of foot traffic combined with the collection of mussels for bait may reduce mussel cover and create mussel-free gaps. To test this hypothesis, the effects of trampling and bait-removal on mussel populations were experimentally examined. Plots in a mussel bed were subjected to monthly combinations of trampling (0, 150, or 300 steps) and simulated bait-removal (0 or 2 removed mussels). Although the experiment was done during a period of high natural disturbance associated with the 1997–1998 ENSO, plots receiving treatments experienced significantly greater reductions in mussel cover, mass, and density than controls. These results indicate that visitor foot traffic and bait-removal by fishers can significantly reduce mussel cover, density, biomass, and sizes.

Introduction

Mytilus californianus Conrad, 1837 communities dominate many wave-exposed shores of the eastern North Pacific (Ricketts et al. 1985). These communities are often made up of a structurally complex matrix of living mussels, shells, sediment, and debris that provide food

and shelter for large numbers of species, with up to 300 species being associated with individual beds (Suchanek 1979), and as many as 750 species in beds distributed throughout the Southern California Bight (Kanter 1979).

Natural disturbances to mussel communities are relatively common. Large gaps within mussel beds are created by strong wave disturbance (Dayton 1971; Paine and Levin 1981; Denny 1987; Menge and Sutherland 1987), log battering (Dayton 1971), heavy fouling (Witman and Suchanek 1984; Denny 1987), ice scour (McCook and Chapman 1991), and predation (VanBalaricom 1987). Small disturbance gaps produced by the removal of a few individuals can recover quickly due to the encroachment of adjacent mussels (Paine and Levin 1981). Large gaps ($> 3 \text{ m}^2$), however, must be recolonized by larvae and can take up to several decades to fully recover (Hewatt 1935; Castenholz 1967; Cimberg 1975; Suchanek 1979, 1981; Paine and Levin 1981; Sousa 1984; Hill et al. 1992).

Anthropogenic impacts, including extraction of mussels, are additional sources of disturbance that can lead to gap formation. Murray et al. (1999) reported that southern Californian rocky shores receive a very high number of visitors during low-tide periods. Mussel beds in these and other areas are impacted by foot traffic and the extraction of mussels for food or fishing bait (Adessi 1994; Brosnan and Crumrine 1994; Murray et al. 1999). At several sites in southern California, mussel cover was found to be lower at sites subjected to a high degree of fisher activity as compared to sites with low fisher activity (Smith 2002). Human use of the intertidal zone may be an important, but little recognized, contributor to decreases in mussel abundances observed in southern California during the past 20 years (Robles 1996; Raimondi et al. 1999; Engle and Davis 2000a, 2000b). Many southern Californian mussel beds have been transformed during this period from thick multi-layered matrices to single- or double-layered beds, characterized by frequent mussel-free gaps dominated by encrusting algae and bare rock (Robles 1996; Smith 2002).

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The purpose of this study was to investigate the impacts of two forms of human disturbance on southern Californian mussel beds: bait collection and foot traffic. To directly test the effects of fisher disturbance, we performed experimental studies to examine the effects of trampling and simulated bait removal on mussel beds. We hypothesized that these activities would decrease mussel cover, biomass, and density.

Materials and methods

A study site in southern California at Monarch Bay was established in an extensive, flat *Mytilus californianus* bed (Fig. 1). Overall human use (e.g. tidepoolers, collectors, walkers) at the site was relatively low (annual mean of 0.05 visitors per 10 m shoreline per 10 min), as was collector use (0.014 collectors per 10 m shoreline per 10 min), as measured during human-use surveys in 1995–1996 (Kido and Murray 2003). During these surveys, observations of human activities were made for five 10-min intervals during low-tide periods four times per month for 1 year at eight sites in our study region. Human use at these sites ranged from 0.05 to 0.95 visitors per 10 m shoreline per 10 min while the number of collectors ranged from 0.009 to 0.113 per 10 m shoreline per 10 min. In addition to overall human use, fisher use at the site was also low (annual mean of 0.01 fishers per 10 m shoreline per 10 min as compared to the highest fisher use site with 0.17 fishers per 10 m shoreline per 10 min, S.N. Murray, unpublished data). Human use was low because of the difficulty in accessing the shore.

A factorial study, using randomized blocks, was performed to assess the effects of trampling and bait removal on mussel communities. Trampling treatments were provided at 3 levels (0, 150, or 300 steps per month), and a simulated bait-removal treatment at 2 levels (0 or 2 mussels removed per month).

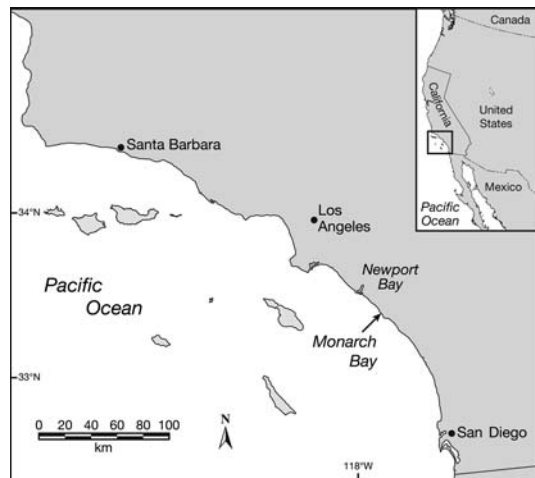


Fig. 1 Location of the study site at Monarch Bay in southern California

Twenty-four 0.35 m² (0.5 m×0.7 m) plots were randomly placed in mussel beds located on large, horizontal rocky surfaces with similar initial mussel cover. Plots were arranged into four homogeneous blocks based on similarities in initial mussel cover, location, and tidal height to account for block-to-block variation that might occur due to spatial gradients in environmental conditions. Each block contained 6 plots that were randomly assigned combinations of simulated bait-removal and trampling treatments (0 steps, – removal; 150 steps, – removal; 300 steps, – removal; 0 steps, + removal; 150 steps, + removal; and 300 steps, + removal). Treatments were repeated monthly for 1 year from June 1997 to May 1998.

For plots that received the bait-removal treatment, ten mussels were chosen randomly. The two largest individuals of the ten were removed each month to simulate fishers who we observed collecting larger mussels for fishing bait. Extracted mussels were returned to the laboratory to determine maximum shell length (MSL) and wet weight (including the shell).

To apply trampling treatments, a 60- to 75-kg person wearing soft-soled shoes walked with a normal stride on plots with either 150 or 300 steps (429 or 857 steps m⁻²), making sure to cover uniformly all areas of the plot. For those plots that received a combination of treatments, simulated bait-removal was applied immediately prior to trampling treatments. These trampling treatments were conservative compared with other intertidal trampling studies (e.g. Brosnan and Crumrine 1994; Brown and Taylor 1999), and are believed to be representative of the density of foot traffic observed on moderately visited mussel platforms in the region.

Prior to the monthly application of trampling and bait-removal treatments, plots were photographed. These photographic records were then used to determine mussel cover by employing a point intercept method (Littler and Littler 1985). Following application of trampling treatments, plots were examined and the number of crushed mussels determined.

At the end of the 12-month experiment, large mussels (> 10 mm), as well as all organisms attached to the mussels or within the mussel matrix, were harvested from plots, placed in plastic bags, preserved in 10% formalin seawater, and returned to the laboratory for analysis. Mussels < 10 mm that were not incidentally harvested, were counted and left in plots to reduce impacts and facilitate recovery. The wet weight, including the shell, and the MSL of each mussel were determined. Any attached or encrusting organisms were removed from mussel shells, and excess water trapped in closed mussels was drained prior to biomass determination.

Statistical analyses

Data sets were examined for variance homogeneity prior to analysis using both Bartlett's and Levene's tests and transformed where necessary to meet parametric criteria.

All data sets were analyzed by using a factorial ANOVA, with the trampling treatments and simulated bait-removal treatments as fixed factors, and blocks as random factors.

Mean size differences among the control plots and the two trampling-only treatments were analyzed using a one-way ANOVA to test for effects of visitor foot traffic on mussel size. In addition, a *t*-test was used to test for differences between the control treatment and the bait-removal-only treatment to detect differences in mean size solely due to the simulated bait-removal. Analyses were separated in order to investigate what each activity alone has on mussel sizes. The MSL data were used to determine the size structure of the mussel populations occurring within plots. Differences in population size frequencies among treatments were analyzed using a χ^2 test.

Results

At the end of the 12-month experimental period, mussel mass (g m^{-2}) varied significantly among treatments (Table 1); there was no significant interaction between the two treatments (Table 1). Mussel mass was greatest in control plots ($6,547.7 \text{ g m}^{-2}$) and decreased by more than 80% ($1,106.1 \text{ g m}^{-2}$) in plots receiving combined bait-removal and 300-step trampling treatments (Fig. 2). The mean density of mussels $> 10 \text{ mm}$ MSL at the end of the experiment was also greatest in control plots (446 m^{-2}), and least (79 m^{-2}) in plots receiving both bait-removal and the 300-step trampling treatment (Fig. 2). Densities of mussels $> 10 \text{ mm}$ MSL were also found to differ significantly among treatments (Table 1); again, an interaction between treatments was not detected (Table 1). The same trend was seen in densities of mussels $< 10 \text{ mm}$ MSL, which ranged from $1,275 \text{ m}^{-2}$ in control plots to 454 m^{-2} in plots receiving both treatments (Fig. 2). However, the factorial ANOVA revealed significant differences ($\alpha=0.05$) only resulting from trampling, and not from bait-removal (Table 1).

At the end of the 12-month experimental period, reductions in mussel cover ranged from 57.5% (bait-removal only treatment) to 78.9% (combined bait-removal and 300-step treatment; Fig. 2). Cover loss varied significantly among treatments (Table 1), but again there was no significant interaction (Table 1). Control

plots also experienced a reduction in mussel cover of 40.8% during the study (Fig. 2). Despite this large decline in control plots, plots receiving bait-removal and trampling treatments lost approximately 20–40% more cover than the untreated plots. An average of 6% of the loss of mussel cover in bait-removal plots could be attributed to the immediate effect of removing two mussels per month, and 15% of the loss in trampled plots due to the crushing of mussels during treatment application. Therefore, only a portion of total cover loss during the study was an immediate, direct result of performing the trampling or bait-removal treatments. The remaining losses occurred during intervals between treatment applications.

The largest mussels found in control plots (maximum MSL = 109.5 mm) at the end of the experiment were much larger than those occurring in plots receiving removal treatments, where the maximum MSL ranged from 102.7 mm (bait-removal-only treatment) to 88.4 mm (bait-removal plus 300-steps treatment). Trampling treatments alone resulted in significant changes in mussel mean MSLs (one-way ANOVA; $P < 0.001$, $MS = 10423$, $F = 53.67$, $df = 2$) at the conclusion of the 1-year study. Plots receiving 300 steps per month contained mussels with a mean MSL of 43.7 mm, a value significantly smaller than mussels from control plots (52.8 mm) or plots receiving 150-step treatments (51.3 mm). As expected, a reduction in the mean MSL of mussels also occurred due to simulated bait-removal treatments alone (*t*-test; $P < 0.001$, $MS = 7702$, $F = 36.41$, $df = 1$).

A χ^2 test revealed significant differences ($P < 0.001$, $\chi^2 = 141.4$, $df = 16$) in mussel size structure following the application of experimental treatments (Fig. 3). Higher frequencies of larger individuals were found in control plots compared with plots receiving combined trampling and bait-removal treatments. Differences between controls and plots receiving only trampling treatments were small, although a shift towards higher frequencies of smaller individuals was found in trampled plots.

Discussion

Mussel beds at southern California mainland and island sites are thought to have declined in abundance in recent years with multi-layered beds becoming transformed

Table 1 Summary of ANOVA Results on untransformed data with trampling and bait-removal as fixed factors and blocks as random factors

	Mussel mass				Mussels density $> 10 \text{ mm}$				Mussels density $< 10 \text{ mm}$				Cover loss			
	df	MS	F	P	df	MS	F	P	df	MS	F	P	df	MS	F	P
Trampling (T)	2	3616232	19.1	$< 0.001^{***}$	2	158982	13.5	$< 0.001^{***}$	2	687374	7.5	0.006^{**}	2	1476	18.4	$< 0.001^{***}$
Removal (R)	1	2150507	11.3	0.004^{**}	1	90197	7.7	0.014^*	1	323700	3.5	0.082 ns	1	565	7.1	0.018^*
Block	3	142721	0.8	0.538 ns	3	74639	6.4	0.005^{**}	3	356983	3.9	0.033^*	3	130	1.6	0.226 ns
T×R	2	83895	0.4	0.651 ns	2	1270	0.5	0.638 ns	2	17128	0.2	0.832 ns	2	148	1.9	0.192 ns

Significance levels: ns no significance, $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

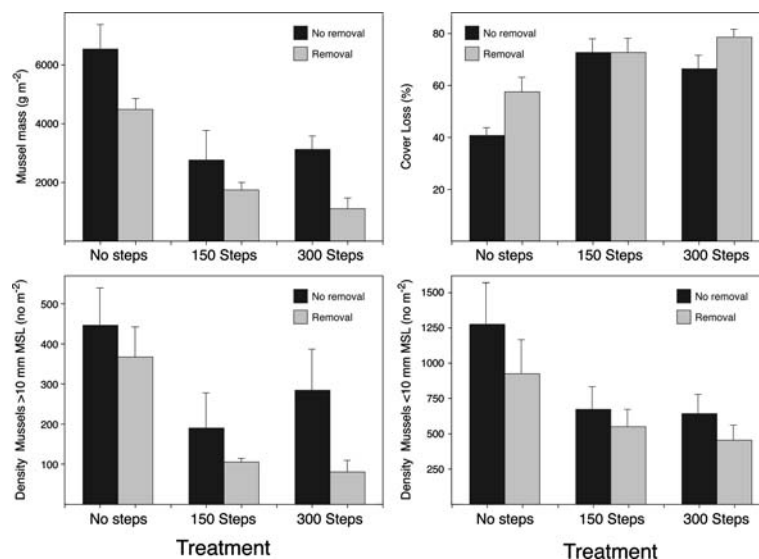


Fig. 2 Summary of mussel mass (g m^{-2}), density (no m^{-2}), and mussel cover loss (%) in experimental plots at the conclusion of the 12-month study. Mussel mass and density were obtained from harvested plots. Mass data include wet weights of biomass plus shells of all individuals >10 mm in MSL. Densities are reported for mussels >10 mm and <10 mm MSL. Cover loss is expressed as the difference in cover from the beginning to the end of the experimental period. Values reported are means (± 1 SE) for indicated parameters for plots that received monthly trampling (0, 150, and 300 steps) and simulated bait-removal ($-$ removal and $+$ removal) treatments

into single-layered beds characterized by frequent gaps (Robles 1996). Mussel mass and density in control plots at Monarch Bay were much lower than values reported for mussel communities in past studies performed in the southern Californian region. Up to 10 times the mussel density and mass found in our control plots were reported for southern Californian mussel beds during the 1970s (Straughan and Kanter 1977; Kanter 1978, 1979; Straughan 1978).

Declines in mussel abundances during the past two decades are thought to be linked to decadal-scale increases in sea-surface temperatures, pollution, and human visitation (Robles 1996). In southern California, the rocky intertidal zone can experience strong disturbance by human visitors (Murray 1998; Murray et al. 1999). Mussels, in particular, are commonly subjected to disturbances such as trampling, and frequently are collected for food and for use as bait by recreational fishers (Ghazanshahi et al. 1983; Addessi 1994; Murray et al. 1999). Our results indicate that mussel beds are disturbed by even low levels of these activities, and that these disturbances may contribute to mussel-bed declines in heavily visited southern Californian habitats. We found that trampling and bait-removal activities can each result in significant decreases in mussel mass, density, cover and MSL, even when conservative trampling (429 and 857 steps m^{-2}) and low-intensity simulated bait-removal treatments (2 mussels per month) are applied. More importantly, the immediate impacts of crushing mussels underfoot and removal of mussels were

overshadowed by the following loss of additional mussels in the time periods between treatment applications.

Recreational fishers frequent rocky shores around the world and often collect bait on site (Blake 1979; Jackson and James 1979; Cryer et al. 1987; Fairweather 1991; Kingsford et al. 1991; Pombo and Escofet 1996; Wynberg and Branch 1997), and may be a large source of trampling disturbance on intertidal organisms. In

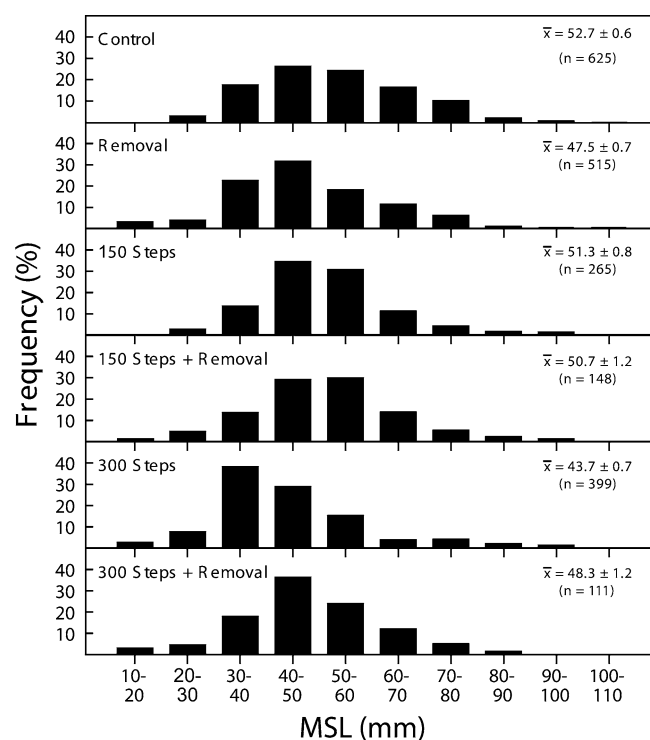


Fig. 3 Size frequency distributions of mussels at the end of the 12-month experimental period. Values are sorted by 10 mm-size class for all mussels >10 mm maximum shell length (MSL). Statistical analysis using a χ^2 test showed significant ($P < 0.001$) differences among treatments. Mean MSLs (± 1 SE) and total sample size are also reported for each treatment

southern California, extraction of mussels for fish bait is a common occurrence (Ghazanshahi et al. 1983; Addressi 1994; Murray et al. 1999). Fisher activity has been shown to be negatively related to mussel cover at southern Californian sites where mussel beds exposed to a high level of recreational fisher use had more gap space and less mussel cover than beds at sites receiving lower fisher use (Smith 2002). Further observations suggest that fisher disturbance is the primary cause for these gaps because mussel beds on outer rocks and other habitats less accessible to fishers at these same sites have fewer gaps within mussel beds (Smith 2002). These results support previous studies (e.g. Blake 1979; Cryer et al. 1987; Kingsford et al. 1991; Pombo and Escofet 1996) that have shown that disturbance from bait-collecting can affect targeted populations. For example, on rocky shores in Australia, an observed decline in the densities of a tunicate commonly harvested for fish bait was correlated with harvesting rates by fishermen (Fairweather 1991). Bait-digging on sandy or muddy shores also resulted in decreased abundances of the target and associated species within the sediment (Jackson and James 1979; Wynberg and Branch 1994, 1997).

The effects of extracting intertidal organisms for food and for bait are comparable because the process of extracting the targeted species is similar. Harvesting organisms for food often results in decreased densities and shifts in the size structures of targeted species (e.g. Branch 1975; McLachlan and Lombard 1981; Olivia and Castilla 1986; Ortega 1987; Lasiak 1991; Keough et al. 1993; Sharpe and Keough 1998), and can result in changes in community composition (Durán and Castilla 1989). Our results show that removal for bait of only two mussels per month in a 0.35 m² area can result in a shift in the size structure of the population if larger mussels are targeted for extraction.

Mussel mass, density, and cover were more strongly impacted by trampling treatments than by simulated bait-removal treatments, which accounted for the immediate loss of only two mussels per plot per month; trampling treatments crushed an average of four mussels per plot during each application. Other studies investigating the effects of trampling on intertidal populations have used trampling treatments equivalent to 333–6,250 steps m⁻² (Povey and Keough 1991; Brosnan and Crumrine 1994; Brown and Taylor 1999; Schiel and Taylor 1999). Brosnan and Crumrine (1994) found more severe mussel cover losses in Oregon during a non-ENSO period. Plots with single-layered mussels lost up to 65% cover from the more extreme trampling treatment (4,167 steps m⁻²) used in their study. They also found that plots with multi-layered mussels lost most of the top layer when trampled but showed no decrease in substratum cover because a bottom layer of mussels remained. Brosnan and Crumrine (1994) concluded that tightly packed mussel beds were less susceptible to trampling compared with mussels aggregated in loose patches.

Trampling has also been shown to be detrimental to other intertidal populations. Barnacles and limpets have repeatedly been shown to be damaged by the effects of foot traffic (Zedler 1978; Beauchamp and Gowing 1982; Bally and Griffiths 1989; Povey and Keough 1991; Brosnan and Crumrine 1994). Experimental trampling of several species of algae and seagrass has also resulted in large decreases in cover and biomass (Zedler 1978; Bally and Griffiths 1989; Povey and Keough 1991; Brosnan and Crumrine 1994; Murray and Denis 1997; Keough and Quinn 1998; Brown and Taylor 1999; Schiel and Taylor 1999; Eckrich and Holmquist 2000; Denis 2003).

A majority of the cover loss observed in our treatment plots was not due to the direct, immediate effects of removing mussels or crushing mussels underfoot, but instead occurred during the period following the application of these treatments. This suggests that an indirect effect of our treatments was the weakening of byssal-thread attachments between adjacent mussels, which increases their susceptibility to wave disturbance (Denny 1987). Brosnan and Crumrine (1994) similarly suggested that trampling may weaken areas of a mussel bed, resulting in losses that would normally not occur during winter storms. In addition, they observed that mussel cover continued to decline for almost a year after their experimental trampling treatments ceased. Gaps formed from natural disturbances have also been shown to cause additional losses of up to 50 times the area created by the initial gap because of weakening in the attachments of surrounding mussels (Dayton 1971; Witman and Suchanek 1984; Paine 1989).

We expected that patchy, single-layered mussel beds, such as those characterizing southern Californian shores at the time of our study, would be highly susceptible to trampling and natural disturbances because they lack the support provided by neighboring mussels within multi-layered, tightly packed beds (Harger 1972; Paine 1974; Denny 1987). Our results supported this prediction. Mussel assemblages among our experimental blocks exhibited different degrees of mussel packing and showed different patterns of cover loss during our study, with more cover loss occurring in plots consisting of loosely packed mussels.

Undisturbed plots showed a marked decrease in cover over the 12-month experimental period, and were strongly affected by large natural changes in mussel beds that occurred throughout the region, corresponding with stressful conditions associated with the 1997–1998 ENSO. During this study, southern California was exposed to unusually warmer temperatures and increased physical disturbances from storm waves. Sea-surface temperatures were anomalously warm, exceeding 19°C from June through November 1997 (Coastal Data Information Program, CDIP Historic Data for Newport Beach; <http://cdip.ucsd.edu>). Southern California also experienced increased frequencies of large swells and storm waves, including several days in February 1997

when storm-wave heights exceeded 3 m (California Swell Model; <http://cdip.ucsd.edu>). In addition, unusually low levels of planktonic productivity occurred in the study region throughout the year (Chlorophyll *a* data from SeaWiFS at <http://oceancolor.gsfc.nasa.gov/SeaWiFS>; CalCOFI at <http://www.mlrq.ucsd.edu/calcofi.html>) reducing food availability to mussels. Historically, ENSO events are characterized by strong physical disturbances due to storm waves, warm sea temperatures, and reduced plankton productivity (Pearcy and Schoener 1987; Lubchenco et al. 1993; Seymour 1996; Lavaniegos et al. 1998). High wave energy can increase mortality in mussels as individuals are torn from rocks (Paine and Levin 1981; Witman 1983; Menge and Sutherland 1987). In addition, *M. californianus* is known to grow most rapidly between 15°C and 19°C, and is stressed and grows more slowly at warmer temperatures (Coe and Fox 1942, 1944; Bayne et al. 1976). Furthermore, mussel food supply, which was likely low throughout the study (Chlorophyll *a* data from SeaWiFS at <http://oceancolor.gsfc.nasa.gov/SeaWiFS>), is the most important factor in determining growth rates and gonadal production (Fox and Coe 1943; Coe 1945). Hence, conditions for mussel survival, growth, and gonadal development were poor during our study.

Corresponding with declines in control plots, large reductions in mussel cover were also observed at four other sites located within 15 km of Monarch Bay during 1997–1998 (Raimondi et al. 1999) and were attributed to disturbance and stress associated with ENSO conditions. Moreover, growth-rate measurements taken for 6 months in early 1998 showed extremely slow growth (approximately 0.07 mm per month; J.R. Smith, unpublished data) and provide additional evidence that environmental conditions were poor for mussels during this period.

This study shows that human collecting and trampling can significantly increase losses in mussel abundance over and above those attributable to natural, abiotic conditions. Even during a period of unusually high natural disturbance, we were able to detect significant effects of our trampling and bait-removal treatments on mussel abundance. Our results indicate that single-layered beds, such as those now found in many parts of southern California, are vulnerable to trampling and bait-removal or other forms of mussel extraction, and that these effects likely contribute to the overall declines in mussel abundances in the region.

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